

THE HORDEUM JUBATUM—CAESPITOSUM— BRACHYANTHERUM COMPLEX IN ALASKA

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INTRODUCTION

The wild barleys *Hordeum jubatum* L. and *H. brachyantherum* Nevski have, until recently, been considered separate species. The two are distinguished principally on the basis of awn length, the former being long-awned and the latter short-awned (figs. 2 and 4). Plants intermediate in awn length (fig. 3) have been classified variously: i.e., 1. as the species *H. caespitosum* Scribn. (Rydberg, 1922; 1932; Anderson, 1959); 2. as *H. jubatum* var. *caespitosum* (Scribn.) Hitchc. (Hultén, 1941–1950; Covas, 1949; Hitchcock, 1950; and others); and 3. as a subspecies of *H. jubatum* (discussed below).

The intermediate taxon has been reported over a wide area. Covas, in his treatment of the American species of *Hordeum*, assigned a number of specimens originating from Mexico northward to Washington and Montana to *H. jubatum* var. *caespitosum* and postulated that they were the result of hybridization between *H. jubatum* and *H. brachyantherum*. Löve (1959) listed *H. jubatum* var. *caespitosum* as a member of an element that has migrated into Manitoba from the West. Hultén (1962) represented the approximate, total range of the taxon as extending from northern Mexico through the western half of the United States and Canada to the coastal regions of southern and south-central Alaska.

Extensive biosystematic work performed recently in Canada has firmly established the hybrid status of the intermediate taxon and has cast some doubt on the separation of the parental taxa. Rajhathy and Morrison (1959; 1961), from studies of karyotype, pairing behavior, and interfertility, reported that *H. jubatum* and *H. brachyantherum* were conspecific. Improved pairing in the F₂ was said to indicate "a tendency for true breeding and stabilization in early generations" (1959).

More recently Bowden (1962) assigned all three taxa to *H. jubatum* (all n=14), conferring subspecific rank upon each as follows: *H. jubatum* L. emend. subsp. *jubatum*, *H. jubatum* L. emend. subsp. *breviaristatum* Bowden (to replace *H. brachyantherum*), and *H. jubatum* L. emend. subsp. \times *intermedium* Bowden (to replace var. *caespitosum*). For the purposes of this paper,¹ however, the nomenclature of Hitchcock will be followed. Bowden reported hybrid swarms in the Canadian prairies that demonstrated clinal variation with the parental taxa and also reported the presence of advanced segregate-populations in North and South Dakota.

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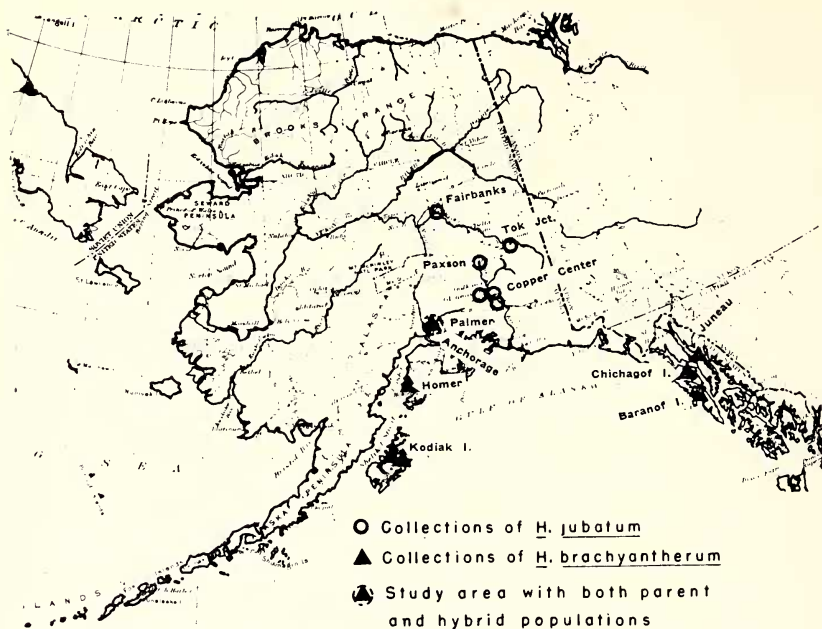


FIG. 1. Collection sites of *H. jubatum*, *H. jubatum* var. *caespitosum*, and *H. brachyantherum*.

The present report concerns the status of the three taxa in their northernmost region of occurrence in the West. The principal study area was in the vicinity of Palmer, Alaska, where hybrid swarms were found occurring with the parental taxa. But in most cases where *jubatum* and *brachyantherum* were found together, hybrids were not apparent. In view of the disposition by Bowden more detailed analyses of these populations were deemed pertinent.

SOURCE OF MATERIALS

The study was confined to Alaskan materials. Population samples of hybrid and parental types were collected around the Knik Arm of Cook Inlet northeast of Anchorage in 1962 and 1963. Other collections of the parental taxa were made in regions where no contact between the two was evident (fig. 1). The latter collections of *brachyantherum* were made in the region of Homer on the Kenai Peninsula, on Kodiak Island, and at Juneau, Chichagof Island, and Baranof Island in southeastern Alaska. Samples of *jubatum* were collected along the highway system of the Alaskan interior: at Atlasta House Lodge, Mile 166, Glenn Highway; Tok Junction, Mile 1314, Alaska Highway; Fairbanks; Paxson Lodge, Mile 186, Richardson Highway; and at Kenny Lake and Copper Center in the Copper River Valley.

Spikes for cytological analysis were collected from plants of *caespitosum* and from adjacent plants of *jubatum* and *brachyantherum* growing at one of the Cook Inlet sites.

DISTRIBUTION AND ECOLOGY

The parental taxa differ markedly in their ranges of distribution in Alaska, although overlapping in a number of areas. The long-awned *jubatum* is widely distributed and well represented in the interior. Generally it is less frequent to rare or absent in the coastal regions. Apparently it does not occur in the arctic region north of the Brooks Range. Though essentially weedy in character, occurring in abundance along roads and around settlements, as remarked by Hultén (1942, p. 267) "(it) must certainly be indigenous in the interior (of Alaska)." Hultén (1962) considers it native both to North America and northeastern Asia. Farrand (1961) reported that the remains of *jubatum* were found in the analysis of stomach contents of a frozen woolly mammoth discovered in northern Siberia.

The short-awned *brachyantherum* is indigenous to North America and some coastal portions of eastern Asia (Hultén, 1941-1950). It is strictly coastal in its Alaskan occurrences, being found inland only along estuaries and inlets. Unlike *jubatum* it is an important component of certain native plant communities that develop on beach meadows and tidewater flats (Hanson, 1951). It also behaves as a weed by invading disturbed ground around settlements.

The hybrid *caespitosum* may be expected to occur wherever the parental taxa meet. We observed it in abundance only in the Cook Inlet region.

The parental taxa demonstrate a distinctive difference in ecology where they meet on beach meadowlands. For instance, *jubatum* occurs on disturbed ground of a picnic area intruding upon meadowland of the Eklutna flats northeast of Anchorage. It is not present, however, in the native meadow community that is immediately adjacent and wherein *brachyantherum* is an important component. Hanson (1951) described this community in some detail. Although there is ample opportunity for pollen exchange between the two taxa in this area, only one small colony of hybrid plants was located. These occurred in the vicinity of an old abandoned dwelling.

The most extensive hybrid swarms were found 1. on a homestead that was established in the middle 1930's (during the early days of agricultural colonization of the Matanuska Valley), and 2. within the town of Wasilla, which was founded about 1916. Several collections also were made in Palmer, the agricultural center of the valley and Matanuska village, a nearly abandoned settlement.

Hybridization appears to have occurred mostly where both parental taxa have been in contact on disturbed ground for a number of years. Indications are that the hybrids are short-lived, so hybridization may

be more frequent than is apparent. Some hybrid colonies located in 1962 were not present in 1963, apparently having succumbed during the winter.

MORPHOLOGICAL ANALYSIS

In the morphological analysis of the three taxa a node bearing its single sessil spikelet and two pediceled lateral spikelets was chosen between one-fourth and one-half the distance up the inflorescence. Often, due to disarticulation of the rachis, only the basal half or less of the inflorescence remained, particularly on *brachyantherum*. The following characters of this group of spikelets were measured or scored: 1. lemma-awn length of the single floret in the central spikelet, always measured from a point on the lemma opposite the tip of the palea, a procedure which ensured consistency of technique but which probably exaggerated the actual length of the awn, 2. palea length of the floret in the central spikelet, 3. internode length of rachis joint attached to spikelet, 4. development of a staminate floret in at least one of the two lateral spikelets, with a well developed palea being accepted as evidence of its development. Other characters measured or scored were: 5. width of penultimate leaf, 6. presence or absence of hairs on upper surface of leaf, 7. depth of cleft on culm at juncture of peduncle and inflorescence—the cleft resulting from a collar that forms an open-necked V of varying depths on one side of the culm at the origin of the inflorescence (fig. 8), 8. features of the lower epidermis of the terminal leaf.

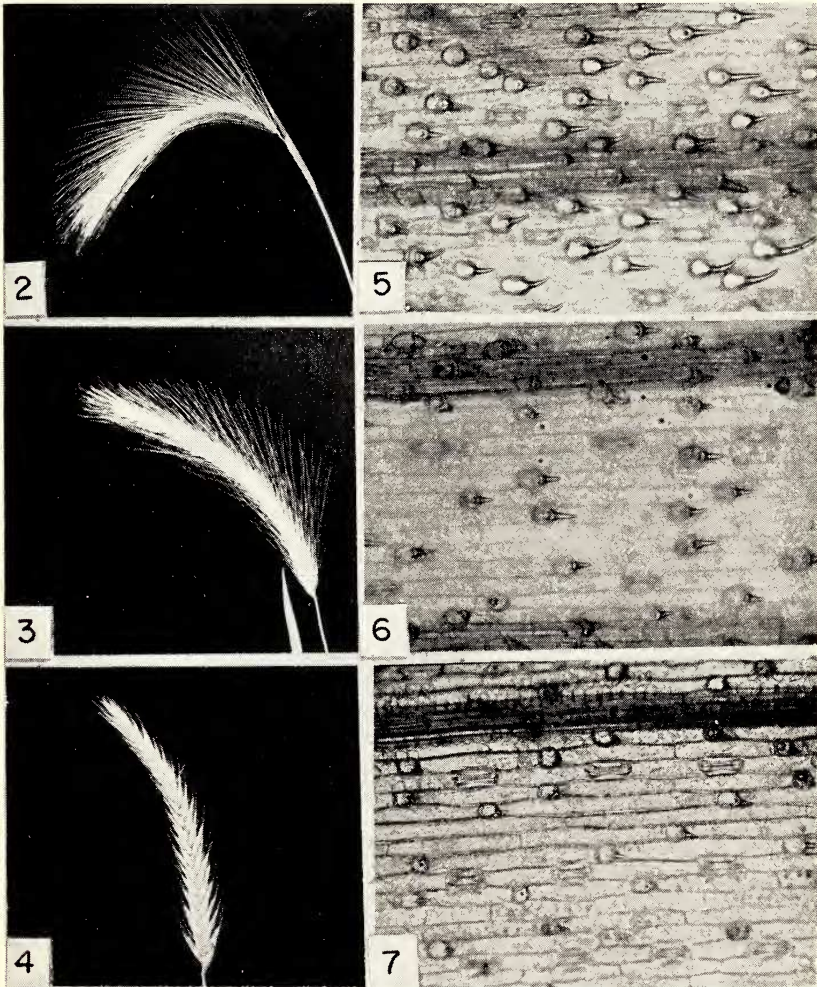
In the analysis of the epidermal features, the three taxa were found to differ principally in the shape and frequency of prickles. The prickles of *jubatatum* were long-barbed and very numerous (fig. 5); those of *brachyantherum* were short-barbed and infrequent (fig. 7); and those of *caespitosum* were intermediate in shape and frequency (fig. 6). While critical measurements were not made of these characters, observations of a number of leaves indicated that *brachyantherum* could be more readily distinguished by this means than could *jubatatum* or *caespitosum*, since the latter two tended to converge in their epidermal features.

Quantitative measurements of spikelets and leaves are summarized in Fig. 8. The delineation of the taxa according to awn length is particularly noteworthy in this summary. Short-awned *brachyantherum* is clearly separated from the other two taxa, and all three populations are widely disjunct in their major portions (i.e., the portion contained in two standard deviations—theoretically, about 68%). In the other measurements the means differ but the ranges of variability overlap for all three taxa. The portions contained in two standard deviations generally overlap, with the most disjunct patterns being registered in leaf width and palea length. The hybrid *caespitosum* essentially is intermediate in its ranges and means for all measurements.

Figure 8 indicates, however, that the extent of overlap in characters is no greater where the parents come in contact and hybridize than it is

for the population as a whole. Indeed, in the cases of palea length and internodal length the portions of the collections from mixed populations included in two standard deviations are even more widely separated than comparable portions of the total parental populations.

The three taxa were further delimited by plotting awn length against palea length (fig. 9) and by determining correlation and regression coefficients of the paired data (table 1). A high positive correlation between awn length and palea length in *brachyantherum*, within a very narrow range of variation in awn length and a broad range of variation in palea



FIGS. 2-7. Inflorescence ($\frac{1}{4} \times$) and leaf epidermis ($125 \times$): 2, 5, *H. jubatum*; 3, 6, *H. jubatum* var. *caespitosum*; 4, 7, *H. brachyantherum*.

TABLE 1. CORRELATION AND REGRESSION COEFFICIENTS OF THE PAIRED VARIABLES LEMMA-AWN LENGTH AND PALEA LENGTH FOR HORDEUM JUBATUM, H. JUBATUM VAR. CAESPITOSUM, AND H. BRACHYANTHERUM

Taxon	Number of specimens included in analysis	Correlation coefficient	Regression coefficient
<i>H. jubatum</i>	184	+ .22	0.09
<i>H. jubatum</i> var. <i>caespitosum</i>	69	+ .32	0.39
<i>H. brachyantherum</i>	210	+ .62	2.77

length, distinguishes it in particular from the other two taxa. These have much lower correlation coefficients within much wider ranges of variation in awn length.

An analysis of the combined data, i.e., treating the data as that of a single taxon, indicated an entirely different relationship between the two variables. Whereas the correlation coefficients were positive when treating the taxa separately, the combined data yielded a negative correlation with a high value of $-.76$ and a regression coefficient of $.40$.

Differences in leaf pubescence contributed to the separation of the shorter-awned hybrid forms from *brachyantherum*. In Figure 9 all but one of the hybrid specimens nearest *brachyantherum* are pubescent on the upper leaf surface, as opposed to the consistently glabrous condition in *brachyantherum*. Both *jubatum* and *caespitosum* varied in this regard.

Figure 9 also demonstrates that all three taxa varied in the development of staminate or sterile lateral spikelets and that plants with longer paleas tended to produce the staminate lateral spikelets. The correlation was much more pronounced in *brachyantherum* than it was in *jubatum*; but because of the difference in magnitude of palea lengths of the two taxa, where the two overlapped in palea lengths they often differed in the character of their lateral spikelets (table 2). Plants of *jubatum* with paleas over 6.5 mm up to the maximum of 7.5 mm tended to produce staminate lateral spikelets, while plants of *brachyantherum* with paleas measuring in the same range generally produced sterile lateral spikelets. Palea measurements ranged up to 10.2 mm in *brachyantherum*.

TABLE 2. PRODUCTION STAMINATE LATERAL SPIKELETS IN SPECIMENS OF HORDEUM JUBATUM, H. BRACHYANTHERUM, AND H. JUBATUM VAR. CAESPITOSUM WITH PALEAS MEASURING FROM 6.6 mm TO 7.5 mm

Taxon	Number of specimens with sterile spikelets	Number of specimens with staminate spikelets
<i>H. jubatum</i>	8	12 = 60%
<i>H. brachyantherum</i>	48	5 = 9%
<i>H. jubatum</i> var. <i>caespitosum</i>	18	16 = 47%

CYTOLOGICAL ANALYSIS

Meiotic studies were conducted of floret material fixed in acetic alcohol (3:1), smeared in acetocarmine, and the correct stages made permanent with Venetian turpentine (Wilson, 1945). Meiosis was found to be highly irregular in the hybrid (figs. 10-13). Because of this it was impossible to obtain detailed pairing relationships between the parental genomes. Metaphase I of the hybrid was particularly disturbed; among 120 cells examined there were none in which chromosome pairing ratios could be ascertained. Practically all were of the types illustrated. Multivalent associations usually appeared (figs. 10 and 11), but neither the number of chromosomes in the association nor their frequency could be definitely determined. Further, it is not certain whether these associations were always due to true pairing or to chromosome stickiness, as suggested by several investigators of interspecific and conspecific hybrids in the genus *Bromus* (Walters, 1954; Nielsen, 1955; Hanna, 1961).

Anaphase I showed some laggards that often seemed to be in multivalent associations (fig. 13). These laggards were manifest as micronuclei at second divisions and in the quartet stage (fig. 12). The unequal timing of second division also is common in cells of the hybrid and may be a further manifestation of abnormal meiosis.

Meiosis was mostly regular in *jubatum* and *brachyantherum* (fig. 14). The frequency of micronuclei, based on observations of 200 cells for each species, was 0.4% in *jubatum* and 0.5% in *brachyantherum*, compared to 13.1% in *caespitosum*. The meiotic irregularities of the hybrid were correlated with a high degree of sterility, as determined by counts of mature caryopses in the central spikelets (table 3). One hybrid plant was found to be quite fertile. The parental taxa were highly fertile.

DISCUSSION

We believe that the data presented here offer little support for combining the Alaskan populations of *H. brachyantherum* with *H. jubatum*. This study reveals 1. marked differences in ecology of the two taxa, 2. an apparent failure of the two taxa to hybridize on many sites where they are in contact, 3. meiotic irregularities and a high degree of sterility in the hybrid intermediate *caespitosum*, 4. a distinct morphological separation of *brachyantherum* from both *caespitosum* and *jubatum* on the basis of awn length, 5. an association of other morphological differences with this difference in awn length, and 6. differences in relationships between characteristics that would appear to be based on fundamental differences in genetic systems.

If *brachyantherum* and *jubatum* are to be considered members of the same species, then *jubatum* would be the long-awned phase and *brachyantherum* the short-awned phase of a mutual genetic system. Accordingly, if awn length is plotted against another characteristic with which it shows correlation, we might expect that variation within one phase

would be a natural extension of variation within the other phase. But when awn length was plotted against palea length, the specimens formed

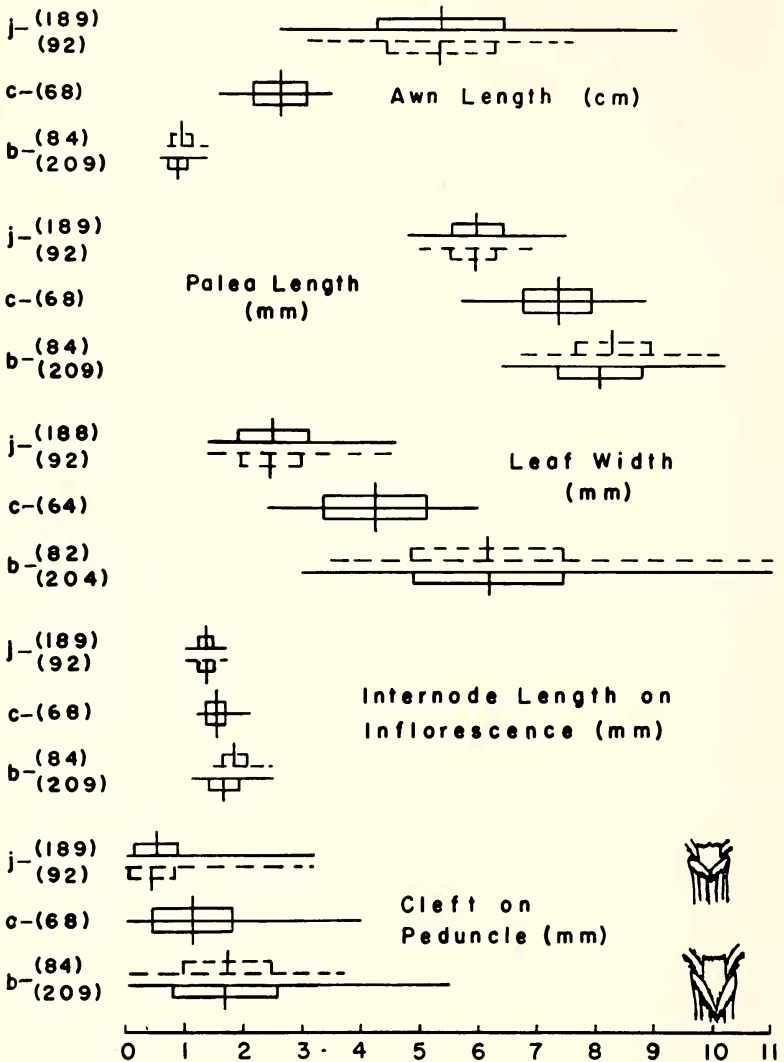


FIG. 8. Summary of morphological analysis of *H. jubatum*, *H. jubatum* var. *caespitosum*, and *H. brachyantherum*. Small letters: *j* = *jubatum*, *c* = *caespitosum*, *b* = *brachyantherum*. Figures in () signify number of specimens analyzed for each character. Horizontal line encompasses total range of variability; vertical line denotes mean; blocked portion comprises two standard deviations. Solid line represents total sample analyzed for each character; dashed line includes only that portion of each parental sample obtained from mixed populations.

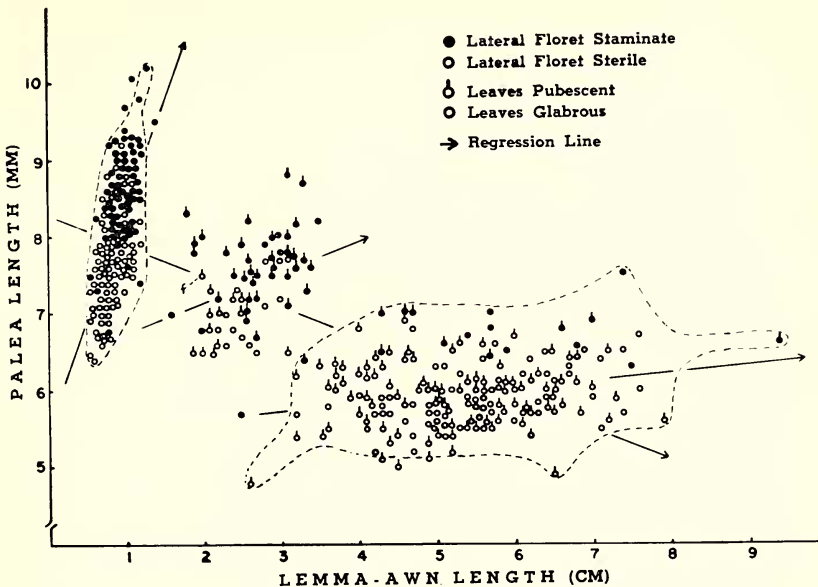


FIG. 9. Graphical comparison of *H. jubatum* (long-awned), *H. jubatum* var. *caespitosum* (intermediate), and *H. brachyantherum* (short-awned). Dashed lines enclose all variants of parental taxa collected in regions where the two were not in contact. See Fig. 8. for numbers of specimens analyzed.

three natural groupings with regression lines that could not possibly be interconnected. An attempt to analyze the data as that of a single taxon produced a result that clearly violated obvious character relationships. The high correlation between awn length and palea length in *brachyantherum*, as opposed to a weak correlation in *jubatum*, and the very different regression coefficients certainly must reflect significantly different genetic systems.

Difficulties of separation that did occur generally involved specimens resembling *jubatum*, whereas the *brachyantherum* component of mixed populations appeared quite distinct. Whatever introgression has occurred has been insufficient, at least at this stage, to have produced intergradation. The propensity for hybridization between *jubatum* and *brachyantherum*, moreover, is insufficient in itself as a criterion for lumping the two. For instance, *H. jubatum* appears to hybridize quite as readily with *Agropyron trachycaulum* (Link) Malte as it does with *H. brachyantherum* in Alaska.

Most specimens of *caespitosum* analyzed for fertility were completely infertile. The representative found to be the most fertile was a short-awned variant (labeled f in fig. 9) nearer to *brachyantherum* than to *jubatum*. The structure of the scatter diagram shows considerable room for the development of specimens with awns longer than in *brachyan-*

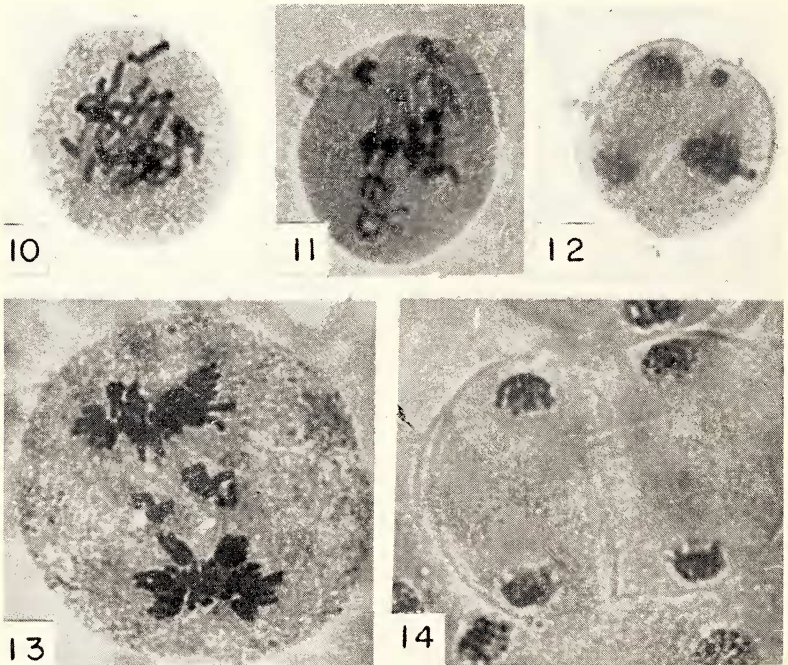
therum and with paleas longer than in *jubatium*. The self-compatibility of these taxa enhances the possibility of a new species being formed in this morphological range, should appropriate reproductive barriers develop (Grant, 1963, pp. 451 ff.). This assumes, of course, that these characters reflect more than morphological differences. Biotic and physical factors of the environment, however, could preclude such a development.

TABLE 3. PERCENT FERTILITY OF HORDEUM JUBATUM, *H. JUBATUM* VAR. CAESPITOSUM, AND *H. BRACHYANTHERUM*

Taxon	No. of Florets	% Fertility	No. of Plants	Range in % Fertility	Median
<i>H. jubatum</i>	666	87.1	10	18.6–100 ¹	89.2
<i>H. jubatum</i> var. <i>caespitosum</i>	1054	3.0	15	0.0–47.0 ²	0.0
<i>H. brachyantherum</i>	543	89.7	13	79.1–100	89.7

¹ One plant of *jubatium* registered 18.6% seed set, otherwise the range was between 86.7% and 100%.

² One plant of *caespitosum* registered 47% seed set, otherwise the range was between 0.0% and 2.0%.



FIGS. 10–14. Meiotic configurations in *Hordeum*: 10–13, meiotic irregularities in *H. jubatum* var. *caespitosum*; 10, 11, Metaphase I; 12, second division; 13, Anaphase II; 14, normal Telophase II in *H. jubatum*.

Apparently the intermediate taxon has achieved a measure of fertility in the Midwest and is able to migrate on its own. With the potential doubtlessly varying from region to region throughout the extensive range of the hybrid, the possibility of its establishment as a species in some portion of its range seems worthy of more serious consideration. The outcome of this development in Alaska would appear as yet to be in doubt, but its present status does not warrant combining *brachyantherum* with *jubatum* for theoretical or practical reasons.

In view of the above we recommend that the hybrid be referred to as *Hordeum* \times *caespitosum* Scribn. (pro sp.). The descriptions of Bowden (1962) for distinguishing his three subspecies apply, with the following modifications on measurements of the floret of the central spikelet:

H. brachyantherum . . . lemma-awn 0.6–1.5 mm, palea 6.4–9.5–(10.2) mm
H. \times caespitosum . . . lemma-awn 1.5–3.5 mm, palea (5.7)–6.5–9.0 mm
H. jubatum . . . lemma-awn (2.6)–3.5–7.5–(9.4) mm, palea 4.8–7.0–(7.5) mm

SUMMARY

Alaskan populations of *Hordeum jubatum*, *H. brachyantherum*, and their hybrid *H. jubatum* var. *caespitosum* were sampled and analyzed morphologically and cytologically. Irregular meiotic behavior in the hybrid was coupled with a high degree of sterility, while the parental taxa were highly regular in meiosis and in most cases highly fertile. Differences in ecology, morphology, and certain character relationships were cited as evidence favoring the continued separation of *H. brachyantherum* and *H. jubatum*, in contraposition to a recent action combining the two. The possibility of the development of a new species in some portion of the extensive range of the hybrid was proposed. It was recommended that the hybrid be designated as *Hordeum* \times *caespitosum* Scribn. (pro sp.).

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NOTES AND NEWS

CONDALIA MEXICANA SCHLECHT. VAR. *PETALIFERA* M. C. JOHNSTON, VAR. NOV.—Varieties a typica differens floribus petala parva caduca habetibus. Holotype: Mexico, Zacatecas, rd to Huejuquilla el Alto, Jalisco, 1 mi w of rd junction 18 mi s of Valparaiso on rd to Mezquitic, Jalisco, near Lat 22° 38' N, Long 103° 48' W, *McVaugh 17675*, Sept. 4-5, 1958 (MICH). This variety is treelike, 6 m tall with a trunk diameter of 20 cm. The fruit is reddish; the flowers are greenish. Only one tree was seen at the type locality. It grew near the summit of a pass at 2100 m in rocky oak-covered mountains. The discovery of this plant supports my recent deemphasis of the significance of the presence or absence of petals in this genus (Brittonia 14:332-368. 1962). It is extremely closely related to *C. mexicana* Schlecht. of the eastern Sierra (Tamaulipas to Guanajuato and Hidalgo, in southern Puebla, and in northern Oaxaca), but its flowers possess minute petals. Its locality, to the west of the range of *C. mexicana* var. *mexicana* and at a much higher elevation, supports its designation as a variety. It also differs from *C. mexicana* var. *mexicana* in the dark olivaceous color of the dried specimen and in the arborescent stature. A collection from Durango (*Palmer 608*, F, GH, UC, US) may also be referable to *C. mexicana* var. *petalifera*. This new variety emphasizes the similarities of *C. mexicana* to the rarely collected petaliferous populations near Guanajuato which have been called *C. velutina* I. M. Johnst. The Zacatecas plant, however, has the narrow bud scales, small fruits, and sparse pubescence of *C. mexicana*. — MARSHALL. C. JOHNSTON, Plant Research Institute and Department of Botany, University of Texas, Austin.